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The effect of site conditions and type of ramet clusters on sexual and asexual ramets of *Solidago* × *niederederi* (Asteraceae)

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Abstract

Spontaneous hybrids between alien and native plant species are alien taxa and they threaten native biodiversity due to their high competitive ability or introgression. Thus, we tested the effect of soil conditions, elevation and type of ramet clusters (clonal clumps of shoots) on sexual and asexual ramets of *Solidago* ×*niederederi*, a hybrid between the invasive alien *S. canadensis* and the native *S. virgaurea*. We also tested the relationships between the size of sexual ramets and habitat conditions in the hybrid and its parental species, based on ten sites in NE and S Poland, respectively. The hybrid and its parental species occurred on mineral soils with a wide range of textures (sand, loamy sand, sandy loam, silty loam and loam) and pH (from strongly acidic to slightly alkaline). Sexual ramet clusters dominated in *S.* ×*niederederi* populations, while the total number of ramets was highest in mixed ramet clusters. The cluster × site interaction had a significant effect on the length and biomass of sexual ramets in hybrid populations. Moreover, we found a significant effect of the taxon × site interaction in the case of biomass of sexual ramets and synflorescences (capitula arranged in panicles). Based on the biomass of sexual shoots and synflorescences, the competitive abilities of the hybrid may be more or less similar to *S. canadensis* or *S. virgaurea* albeit depending on site conditions.

Keywords

alien species, biomass production, clonal plants, hybridisation, soil conditions, *Solidago*

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Introduction

Hybridisation between alien and native plant species is well documented worldwide and it is understood as a mechanism of both biological invasion and biotic homogenisation (Vilà et al. 2000; Daehler and Carino 2001; Vallejo-Marín and Hiscock 2016). Plant hybrids of alien-native origin have to be treated as alien taxa (Pyšek et al. 2004), while their impact on native species and ecosystems varies (Volery et al. 2020). Generally, short-lived and sterile hybrids are not harmful, even if they arise frequently in the wild (Pliszko and Kostrakiewicz-Gierałt 2018b), whereas vigorous and fertile hybrids can cause losses of native species with negative effects on ecosystem functions (Daehler and Strong 1997; Ayres et al. 2004).

The ability of alien-native hybrids to produce relatively high biomass indicates their competitiveness, as well as invasive potential (Li et al. 2016). However, biomass production in plant hybrids depends on both genetic and environmental factors. Some hybrids between closely-related species are superior to their parents in terms of biomass, growth rate, viability and disease resistance (Wu et al. 2021), while other hybrids have reduced performance due to genetic incompatibility. Some hybrids show reduced root formation, impaired nutrient absorption, lower shoot biomass and unsuccessful reproduction (Chen et al. 2013; Calvo-Baltanás et al. 2021). The most important abiotic factors influencing plant growth are soil moisture and soil nutrient availability, as well as soil and air temperature, precipitation, photoperiod and solar radiation (Chatzistathis and Therios 2013; Upadhyay et al. 2022). Determining the environmental factors that enhance the biomass production of alien-native hybrids may help to delineate the habitats that are most vulnerable to their establishment and invasion, as well as in developing methods for controlling invasive hybrids.

Solidago ×*niederederi* Khek (Asteraceae), a natural hybrid between North American *S. canadensis* L. and European *S. virgaurea* L., is one of the most frequently-noted alien-native hybrids in Europe in recent years (Pliszko and Zalewska-Gałosz 2016; Skokanová et al. 2020, 2022). The biomass production of *S.* ×*niederederi* as well as the influence of environmental conditions on morphological features and clonal structure of the hybrid (sexual and asexual ramets) have not been studied so far. Interestingly, Karpavičienė and Radušienė (2016) documented that the chemical composition of the soil (pH and the content of organic C, P_2O_5 and potassium) had no significant effect on maximal stem height and plant cover variation amongst the hybrid and parental species populations in Lithuania. Moreover, Baranová et al. (2022) demonstrated that the height and biomass of shoots of *S. canadensis* were higher in the stands with a heavy degree of its invasion (abundance > 50%), showing a self-growth-reinforcing feedback. Similarly, Karpavičienė and Radušienė (2016) found a positive correlation between ramet height and stand cover in *S. canadensis* and *S. gigantea*, but not in *S.* ×*niederederi*.

We: (i) investigated the effect of site conditions and types of clonal clusters (clumps of sexual and asexual ramets) on the length and biomass of shoots and synflorescences (capitula arranged in panicles) in populations of *S.* ×*niederederi* occurring in two different regions of Poland, (ii) tested the hypothesis that the length and biomass of ramets and synflorescences increase with the number of ramets in the clusters of the

hybrid and (iii) determined the competitive ability of the hybrid against its parental species, based on the length and biomass of sexual ramets and synflorescences concerning habitat conditions.

Methods

Study species

Solidago ×*niederederi* is a perennial plant forming small clonal clusters of ramets (clumps of shoots) similar to *S. virgaurea*, but with a greater number of shoots. The phenotype is intermediate between *S. canadensis* and *S. virgaurea* (Fig. 1), especially in shoot height, synflorescence size and shape, involucre size and leaf shape and venation (Nilsson 1976; Gudžinskas and Žalneravičius 2016). The seeds are easily dispersed by wind and show high germination (Pliszko and Kostrakiewicz-Gierałt 2017). However, the number of well-developed fruits (with viable seeds) is usually low, partially due to reduced pollen viability (Migdałek et al. 2014). Vegetative reproduction is rather limited due to a lack of long rhizomes and may happen by detachment of resting buds from the basal parts of the shoots (Pliszko and Kostrakiewicz-Gierałt 2017). Interestingly, the hybrid forms three types of clonal ramet clusters, i.e. sexual, mixed and asexual clusters. The sexual clusters consist of shoots that produce synflorescences, whereas the asexual clusters do not produce synflorescences (Fig. 1). The mixed clusters consist of both sexual and asexual shoots. Moreover, the asexual shoots have a characteristic rosette-like clustering of leaves at the top (Gudžinskas and Žalneravičius 2016) and are noticeably shorter than sexual shoots (Pliszko and Kostrakiewicz-Gierałt 2019).

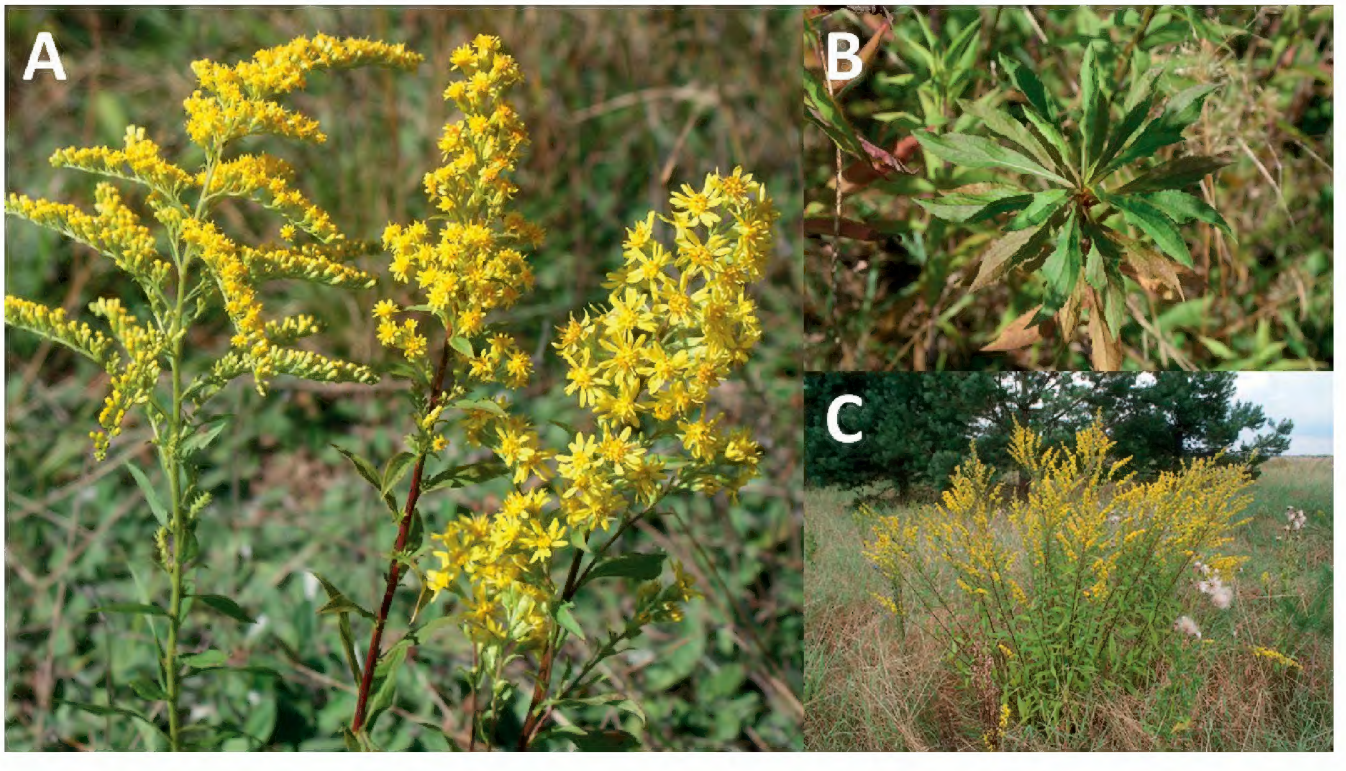

Figure 1. Selected morphological features of *Solidago* ×*niederederi* and its parental species **A** synflorescences (capitula arranged in panicle) of *S. canadensis* (left), *S.* ×*niederederi* (middle) and *S. virgaurea* (right) **B** asexual ramet of *S.* ×*niederederi* **C** cluster of sexual ramets of *S.* ×*niederederi*. Photographed by Artur Pliszko.

Study area and sampling

Field surveys were conducted in Poland (Central Europe) during the flowering period of *Solidago* ×*niederederi* and its parental species, in August and September 2020. A total of 20 sites in two regions in Poland with different climatic conditions and elevation were selected: ten in the north-eastern (NE) and ten in the southern (S) part of Poland (Fig. 2, Suppl. material 1: table S1). The GPS coordinates and elevation of the study sites were determined using a Garmin GPSmap 62st. The sites were located in lowland (NE) and lowland-upland (S) areas of Poland, in the temperate climate zone, showing a higher average annual air temperature and higher average annual precipitation in S Poland than in the NE region. For example, in Kraków (S Poland), the average annual air temperature and annual precipitation were 8.9 °C and 673 mm, respectively, whereas in Suwałki (NE Poland), these parameters reached 7.2 °C and 607.1 mm, respectively, in 1991–2020 (https://klimat.imgw.pl/pl/climate-normals). Moreover, the elevation

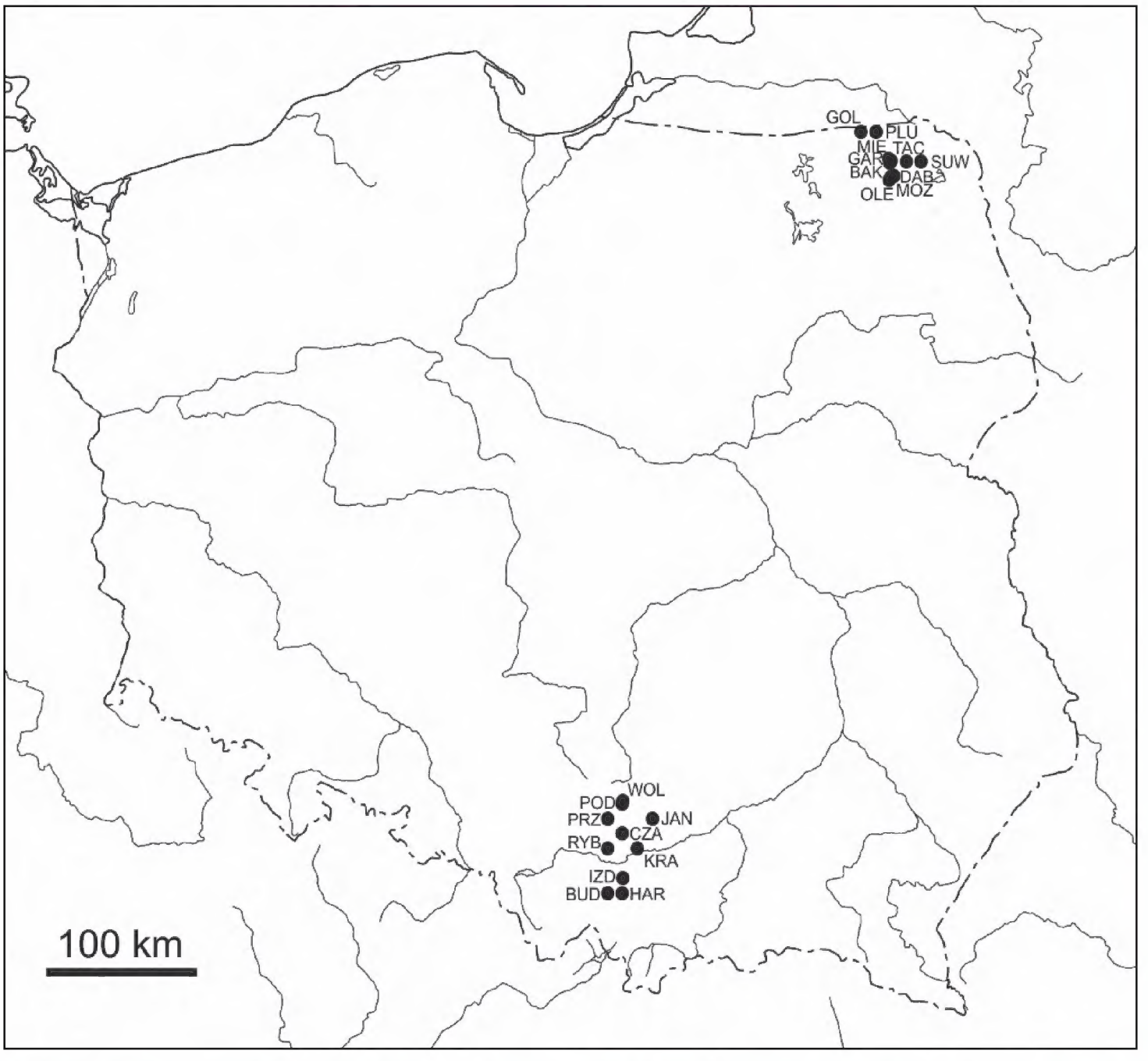

Figure 2. Localisation of study sites of *Solidago* ×*niederederi* and its parental species in Poland. Abbreviations are explained in Suppl. material 1: table S1.

was significantly higher in the S sites than in NE ones (U = 0.00; $p < 0.001$). The sites were mainly occupied by semi-natural and anthropogenic vegetation, showing a high light availability, except the site MOZ which was moderately shaded. In each study site, the hybrid grew together with both parental species and all three taxa were identified, based on morphological features provided by Nilsson (1976) and Gudžinskas and Žalneravičius (2016).

In each study site, the following types of sampling were performed: (1) ten sexual ramets (flowering shoots) of each taxon (the hybrid and its parental species) were randomly selected for comparative biometric study, (2) all clonal clusters of shoots of the hybrid were investigated for structure and biometric study and (3) five soil samples were randomly selected for physicochemical soil study. In each case, the area of sampling was about 0.5 ha. The comparative biometric study included field measurements of the length and biomass of the shoots and synflorescences (fresh material). The structure and biometric study of the hybrid included field measurements of the length and biomass of the shoots (fresh material) in sexual, mixed and asexual ramet clusters, the length and biomass of the synflorescences (fresh material) in sexual and mixed ramet clusters, as well as the number of shoots within the ramet clusters. The length of the shoot (ramet) was measured from the basal part to the top, whereas the length of the synflorescence was measured from the base of the lowest secondary branch with developed capitula to the top. The biomass was measured using a field scale with an accuracy of 0.05 g. The soil samples (each of about 0.5 kg) were collected from the top of the soil (up to 10 cm depth), using a field soil spatula and plastic bags.

Soil analyses

The soil samples were air-dried at room temperature and sieved using a 2-mm sieve. The analyses included the soil texture, pH, content of organic carbon, total nitrogen and available phosphorus (P_2O_5). The granulometric composition was determined using the areometric method of Bouycous and Cassagrande as modified by Prószyński (Polish Standard 1998). The pH of the soil was determined using the potentiometric method in 1M KCl. The content of organic carbon was determined, based on the Tiurin method, total nitrogen based on the Kjeldahl method and available phosphorus based on the Egner-Rhiem method (Ostrowska et al. 1991).

Statistical analyses

The Mann-Whitney U test was applied to test the statistical significance of differences in elevation between the NE and S sites. The Student T-test was calculated to test differences in soil pH, P_2O_5, carbon and nitrogen between the NE and S sites. The interactive chi-square calculator (Preacher 2001) was used to check the statistical significance of differences in the content of sand, silt and clay in soil between the NE and S sites. The mixed linear model was used to test the statistical significance of differences in: (i) number of sexual, asexual and mixed ramet clusters, (ii) number of ramets in

sexual, asexual and mixed ramet clusters, (iii) number of sexual ramets in sexual and mixed clusters, (iv) number of asexual ramets in asexual and mixed clusters, (v) length and biomass of sexual ramets in sexual and mixed clusters, (vi) length and biomass of asexual ramets in asexual and mixed clusters and (vii) length and biomass of synflorescences in sexual and mixed clusters between the NE and S sites of *S.* ×*niederederi*. In this model, the number, the length and the biomass of ramets, as well as the length and biomass of synflorescences, were dependent variables, whereas the type of cluster (defined as a fixed factor) and the site (defined as a random factor) were explanatory variables. For statistical significance, a Tukey test was applied.

A mixed linear model was used to test the statistical significance of differences in the length and biomass of sexual ramets and synflorescences between the NE and S sites of the hybrid and its parental species. In this case, the biomass and the length of sexual ramets and synflorescences were dependent variables, whereas the taxon (defined as a fixed factor) and the site (defined as a random factor) were explanatory variables. Moreover, the Spearman coefficient ($p \leq 0.05$) was used to test the occurrence of correlations between ramet features and abiotic conditions in populations of *S.* ×*niederederi* and its parental species. All statistical analyses were performed using STATISTICA 13.3.

Results

Soil conditions of study sites

The soils were represented by loamy sand, sand, sandy loam, silty loam and loam (Suppl. material 1: table S2). The share of sand in the soil was significantly higher in NE sites than in S sites, whereas the share of silt and clay in the soil was significantly higher in S sites than in NE sites ($\chi^2 = 6.08$, $p \leq 0.05$). The soil pH (from strongly acidic to slightly alkaline) was significantly higher in NE sites than in S sites ($T = 5.73$, $p < 0.001$). Moreover, the content of P_2O_5, C and N in the soil was significantly higher in NE sites than in S sites ($T = 9.19$, $p < 0.001$; $T = 1.98$, $p \leq 0.05$; $T = 2.53$, $p \leq 0.05$, respectively).

Structure of ramet clusters in *Solidago* ×*niederederi*

The mean number of clusters and ramets in hybrid populations is presented in Table 1. In NE and S sites, the number of sexual clusters was higher than the number of mixed and asexual clusters ($F = 44.32$, $p > 0.02$). Moreover, a significant cluster × site interaction on the number of ramets was noticed ($F = 4.14$, $p > 0.02$). There was also a significant difference between the highest number of ramets observed in mixed clusters in NE sites and other types of clusters, excluding sexual clusters in NE sites ($p = 0.86$). However, the number of sexual ramets in sexual and mixed clusters, as well as the number of asexual ramets in asexual and mixed clusters, did not differ significantly in both NE and S sites.

Table 1. Differences in the number of clusters and ramets (mean ± SD) in populations of *Solidago ×niederederi* in north-eastern (NE) and southern (S) regions in Poland. Asterisk indicates the statistical significance level (mixed linear model) of $p \leq 0.05$, ns indicates not significant. The different letters in the superscript indicate the statistical differences (Tukey test).

Type of cluster	Region	Number of clusters	Number of ramets	Number of sexual ramets	Number of asexual ramets
sexual	NE	14.4 (±9.0)^{abc}	51.4 (±29.6)^{abcde}	51.4 (±29.6)	-
	S	12.6 (±6.2)^{abce}	36.9 (±21.3)^{abdef}	36.9 (±21.3)	-
mixed	NE	9.4 (±6.0)^{abcdef}	84.8 (±48.9)^{ac}	54.0 (±30.3)	30.8 (±20.6)
	S	4.6 (±4.1)^{cdef}	26.8 (±28.2)^{abdef}	15.7 (±15.2)	11.1 (±15.4)
asexual	NE	5.2 (±4.0)^{bcdef}	15.5 (±19.2) ^{abdef}	-	15.5 (±19.2)
	S	2.1 (±3.4)^{cdef}	4.1 (±5.3)^{bdef}	-	4.1 (±5.3)
The statistical significance level		$F_{cluster} = 44.3^{*}$	$F_{cluster} = 3.4^{ns}$	$F_{cluster} = 0.6^{ns}$	$F_{cluster} = 7.2^{ns}$
		$F_{region} = 13.9^{ns}$	$F_{region} = 3.4^{ns}$	$F_{region} = 4.9^{ns}$	$F_{region} = 14.0^{ns}$
		$F_{cluster \times region} = 0.3^{ns}$	$F_{cluster \times region} = 4.1^{*}$	$F_{cluster \times region} = 2.3^{ns}$	$F_{cluster \times region} = 0.6^{ns}$

Structure of ramet clusters and abiotic conditions in *Solidago ×niederederi*

In NE sites, the number of ramets in mixed clusters was positively correlated with share of sand (r_s = 0.65) and negatively correlated with the share of silt (r_s = -0.65). Moreover, the number of sexual ramets in mixed clusters was positively correlated with the proportion of sand (r_s = 0.67) and negatively with the proportion of silt (r_s = -0.68).

In S sites, the number of sexual clusters was positively correlated with elevation (r_s = 0.71), the number of mixed clusters was positively correlated with soil pH (r_s = 0.69) and the number of asexual clusters was negatively correlated with elevation (r_s = -0.72) and positively with soil pH (r_s = 0.77). The number of ramets in mixed clusters was positively correlated with soil pH (r_s = 0.66) and the number of ramets in asexual clusters was negatively correlated with altitude (r_s = -0.81) and positively with soil pH (r_s = 0.75). The total number of asexual ramets was positively correlated with soil pH (r_s = 0.81). The number of asexual ramets in mixed clusters was positively correlated with soil pH (r_s = 0.72) and the number of asexual ramets in asexual clusters was negatively correlated with elevation (r_s = -0.81) and positively with soil pH (r_s = 0.75).

Ramet size and structure of ramet clusters in *Solidago ×niederederi*

The cluster × site interaction had a significant effect on the length (F = 49.28, $p < 0.001$) and biomass (F = 5.10, $p > 0.02$) of sexual ramets. The significantly highest values of length and biomass of sexual ramets were achieved by sexual clusters in S sites and the lowest biomass of sexual ramets was found in mixed clusters in NE sites (Figs 3, 4). The Tukey test confirmed that the length and biomass of sexual ramets in sexual clusters in S sites differed significantly ($p < 0.001$) from those of sexual clusters in NE sites, as well as from those of mixed clusters in both groups of sites. The significant effect of the site on the length of asexual ramets was also noticed (F = 11.08, $p < 0.001$). In both mixed and asexual clusters, significantly longer asexual ramets were observed in S sites (Fig. 3). However, the biomass of asexual ramets was similar in mixed and asexual clusters in

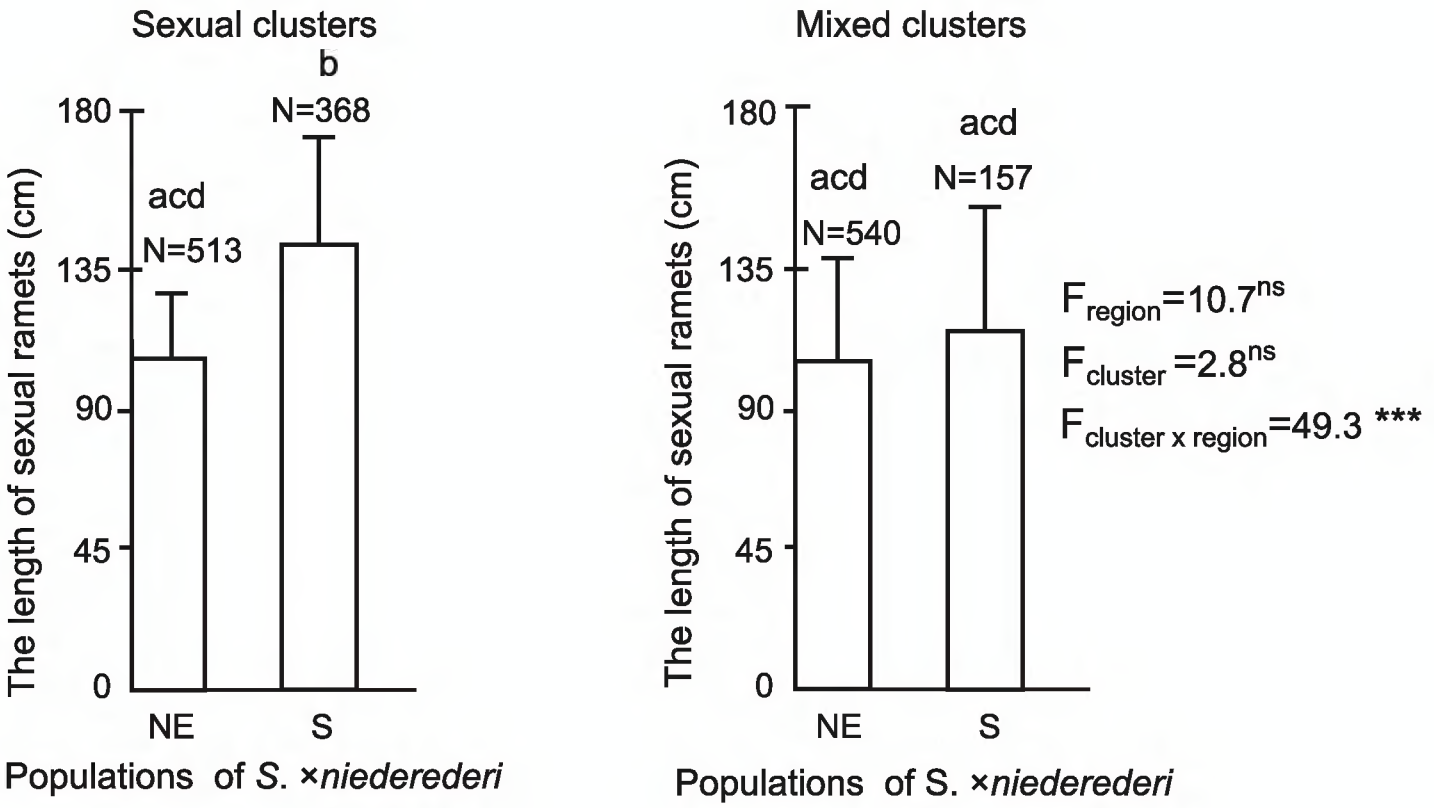

Figure 3. Differences in the length of sexual and asexual ramets between sexual, mixed and asexual clusters in north-eastern (NE) and southern (S) populations of *Solidago* ×*niedereder* in Poland. Asterisks indicate the statistical significance level (mixed linear model): * $p \leq 0.05$, *** $p < 0.001$, ns – not significant. The different letters above the boxes mean the statistical differences (Tukey test).

both NE and S sites (Fig. 4) and the cluster × site interaction was not found. Moreover, the differences in the length and biomass of synflorescences between NE and S sites, as well as between sexual and mixed clusters (Fig. 5), were statistically insignificant.

In NE sites, the length of asexual ramets was negatively correlated with the total number of ramets in mixed clusters (r_s = -0.68), as well as with the number of asexual

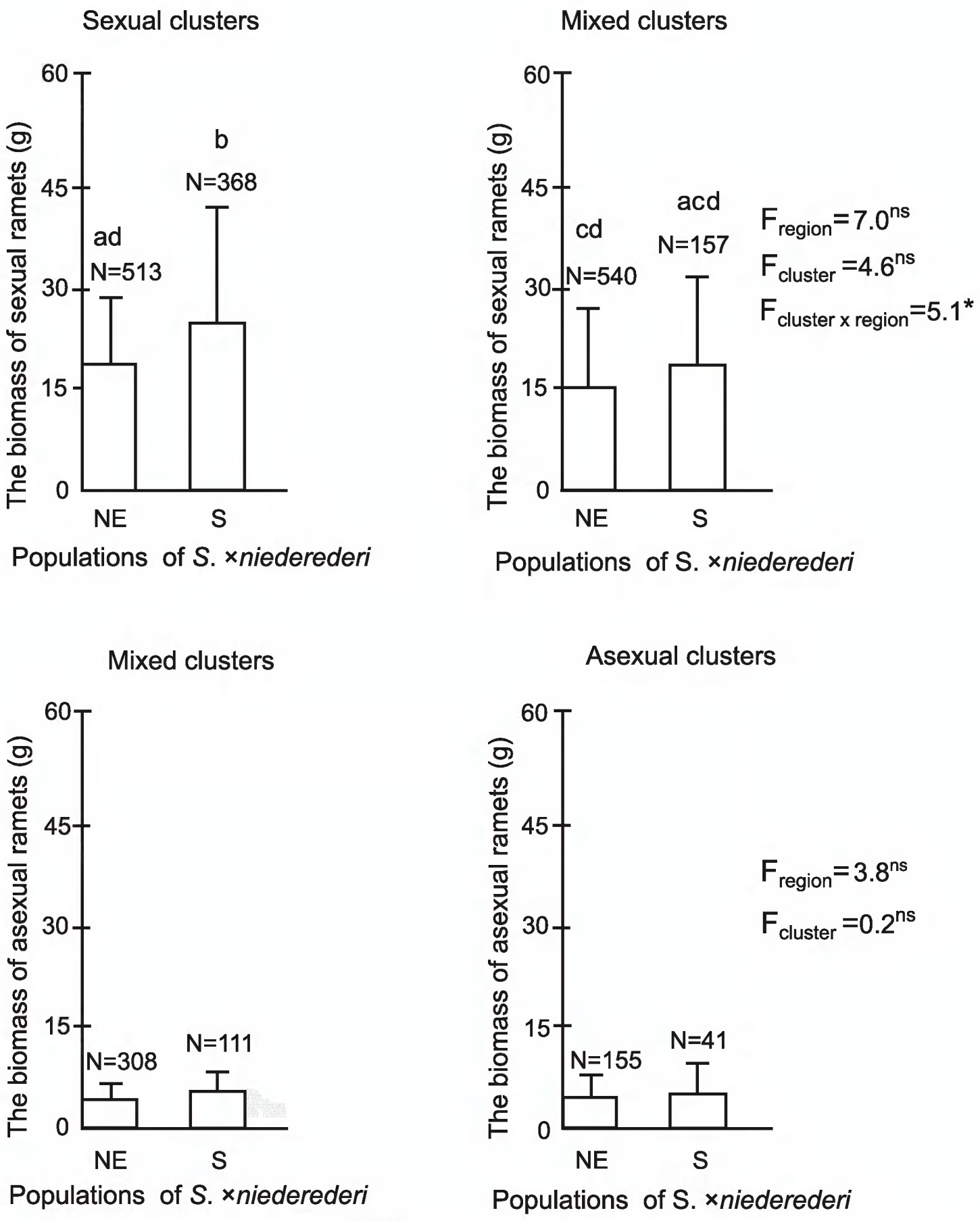

Figure 4. Differences in the biomass of sexual and asexual ramets between sexual, mixed and asexual clusters in north-eastern (NE) and southern (S) populations of *Solidago ×niederederi* in Poland. Asterisk indicates the level of statistical significant $p \leq 0.05$, ns– not significant. The different letters above the boxes mean the statistical differences (Tukey test).

ramets in mixed clusters (r_s = -0.73). In S sites, the length of sexual ramets was negatively correlated with the number of sexual ramets in mixed clusters (r_s = -0.67) and the biomass of sexual ramets was negatively correlated with the total number of ramets in

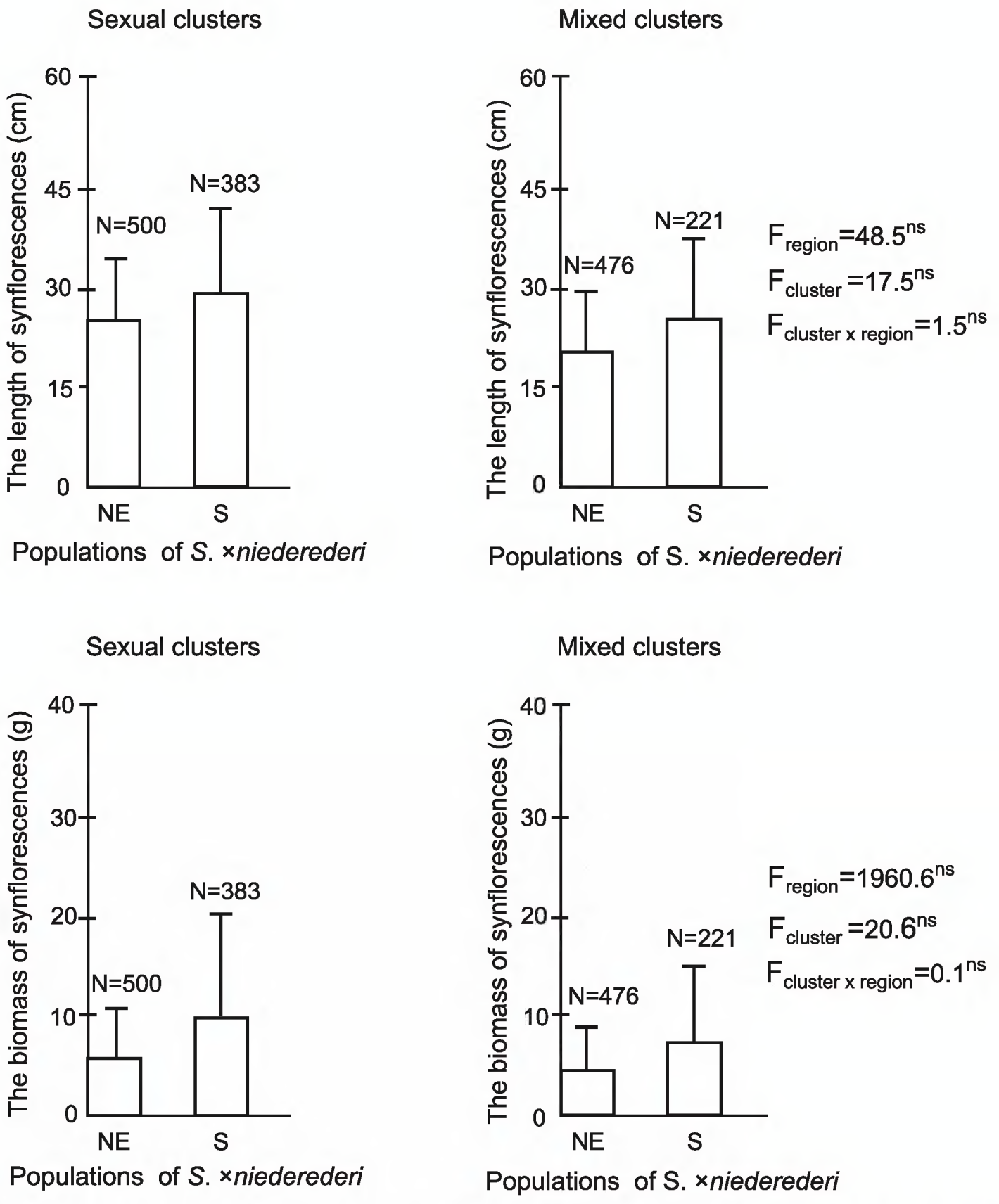

Figure 5. Differences in the length and biomass of synflorescences between sexual and mixed clusters in north-eastern (NE) and southern (S) populations of *Solidago* ×*niedererderi* in Poland. ns indicates not significant.

mixed clusters (r_s = -0.65), as well as with the number of sexual ramets in mixed clusters (r_s = -0.74). Moreover, the correlation between the length of synflorescences and the number of sexual ramets in sexual and mixed clusters was insignificant in NE and S sites. Similarly, there was no significant correlation between the biomass of synflorescences and the number of sexual ramets in sexual and mixed clusters in both groups of populations. Given this, our hypothesis that the length and biomass of ramets and synflorescences increase with the number of ramets in the clusters should be rejected.

Ramet size and abiotic conditions in *Solidago ×niederederi*

In NE sites, the biomass of sexual ramets in mixed clusters was negatively correlated with soil pH (r_s = -0.79), the length of asexual ramets in mixed clusters was positively correlated with the share of sand (r_s = 0.70) and negatively correlated with the share of silt (r_s = -0.71). Moreover, the biomass of asexual ramets in mixed clusters was negatively correlated with soil pH (r_s = -0.63), the length of synflorescences in mixed clusters was negatively correlated with soil pH (r_s = -0.73) and the biomass of synflorescences in mixed clusters was positively correlated with elevation (r_s = 0.65) and negatively correlated with soil pH (r_s = -0.85).

In S sites, the length of asexual ramets in asexual clusters was negatively correlated with elevation (r_s = -0.64), whereas the biomass of asexual ramets in asexual clusters was positively correlated with the share of P_2O_5 (r_s = 0.76).

Size of sexual ramets and synflorescences in the hybrid and its parental species

The tallest sexual ramets were found in *S. canadensis* and the shortest in *S. virgaurea* (Table 2). The differences in the length of sexual ramets between the hybrid and its parental species were statistically significant (F = 96.52, p < 0.001). In addition, the Tukey test showed that the length of sexual ramets of *S. canadensis* was significantly higher in S sites than in NE sites (p < 0.001). In contrast, the length of synflorescences did not differ between the taxa and sites, as well as the taxon × site interaction was not confirmed. Nevertheless, the significant effect of the taxon × site interaction was found in the case of biomass of sexual ramets (F = 9.00, p < 0.001) and synflorescences (F = 7.05, p < 0.001). The highest values of biomass were achieved by *S. canadensis* in S sites and the lowest by *S. ×niederederi* in NE sites. The Tukey test confirmed that the biomass of sexual ramets and synflorescences of the hybrid in NE sites differed remarkably from *S. canadensis* in S sites (p < 0.001), as well as from *S. virgaurea* in NE and S sites (p ≤ 0.05). Moreover, synflorescences of *S. ×niederederi* were significantly heavier in S sites than in NE sites (p ≤ 0.05).

Table 2. Differences in the length and biomass of sexual ramets and synflorescences (mean ± SD) in populations of *Solidago ×niederederi*, *S. canadensis* and *S. virgaurea* in north-eastern (NE) and southern (S) regions in Poland. Asterisks indicate the statistical significance level (mixed linear model): ** p < 0.01, *** p < 0.001, ns indicates not significant. The different letters in the superscript indicate the statistical differences (Tukey test).

Taxon	Region	Sexual ramet length (cm)	Sexual ramet biomass (g)	Synflorescence length (cm)	Synflorescence biomass (g)
Solidago ×niederederi	NE	105.8 (±26.1)^{a}	19.4 (±13.1)^{a}	24.7 (±10.3)	6.7 (±6.1)^{ac}
	S	111.5 (±25.3)^{a}	24.8 (±19.2)^{a}	29.6 (±13.8)	11.2 (±12.7)^{cef}
Solidago canadensis	NE	115.9 (±29.0)^{b}	26.7 (±17.0)^{b}	27.2 (±10.2)	9.4 (±6.3)^{abcef}
	S	146.0 (±27.4)^{e}	51.5 (±31.3)^{c}	32.8 (±11.8)	18.7 (±16.2)^{d}
Solidago virgaurea	NE	88.1 (±21.1)^{d}	20.8 (±14.8)^{a}	34.5 (±15.9)	11.2 (±11.8)^{bcf}
	S	92.2 (±21.4)^{d}	20.2 (±12.7)^{a}	34.8 (±14.2)	11.2 (±8.9)^{bcef}
The statistical significance level		F_{taxon} = 96.5**	F_{taxon} = 10.3^{ns}	F_{taxon} = 7.2^{ns}	F_{taxon} = 1.9^{ns}
		F_{region} = 7.1^{ns}	F_{region} = 2.1^{ns}	F_{region} = 4.7^{ns}	F_{region} = 3.3^{ns}
		$F_{taxon \times region}$ = 2.0^{ns}	$F_{taxon \times region}$ = 9.0***	$F_{taxon \times region}$ = 2.4^{ns}	$F_{taxon \times region}$ = 7.6***

In NE sites, the length of synflorescences of *S. canadensis* was positively correlated with the share of clay (r_s = 0.73). Moreover, in S sites, the length of sexual ramets of *S. canadensis* was positively correlated with the share of sand (r_s = 0.65).

Discussion

Habitat requirements of the hybrid and its parental species

Solidago ×niederederi and its parental species occurred on a wide range of soil pH and texture. Interestingly, similar soil conditions were documented not only in places where the hybrid co-existed with parental species, but also where parental species occurred separately (Karpavičienė and Radušienė 2016). Generally, *S. canadensis* and *S. virgaurea* show a wide tolerance to soil texture and fertility, but the range of soil pH and moisture is usually wider in *S. virgaurea* (Werner et al. 1980; Zarzycki et al. 2002; Szymura and Szymura 2013). Regions with large areas of abandoned fields, with sandy and loamy soils, seem to be particularly prone to the naturalisation of *S. ×niederederi*, as in the case of *S. canadensis* (Szymura and Szymura 2013; Perera et al. 2021). It is also relevant to mention that the high probability of the hybrid occurrence in Europe has been predicted in areas with an annual temperature range of 18–30 °C and a minimum temperature of the coldest month close to or slightly higher than -10 °C (Jaźwa et al. 2018). The vertical distribution of *S. ×niederederi* is rather narrower than wide as both parental species are mainly restricted to lowlands and highlands, where they form the most abundant populations (Szymura and Szymura 2013; Kiełtyk and Mirek 2014; Perera et al. 2021).

Structure of ramet clusters in *Solidago ×niederederi*

In this study, we showed that sexual clusters dominated in *S. ×niederederi* populations, but the total number of ramets was the highest in mixed clusters. Similar results were obtained in previous studies (Pliszko and Kostrakiewicz-Gierałt 2017, 2019). Moreover, we found a significant effect of the cluster × site interaction on the number of ramets. Most likely, the differences in the structure of the hybrid clones were related to their different age, as well as to environmental conditions. The ability to form numerous sexual ramets makes the hybrid competitive with other plants (including parental species) in terms of attracting pollinators and colonising new areas by seeds. Observations made in a domestic garden confirmed that the capitula of *S. ×niederederi* are readily visited by many insects (Pliszko and Kostrakiewicz-Gierałt 2018a). Additionally, the formation of numerous generative shoots can contribute to the hybrid's reproductive success and further spread, especially since its pollen grains have a reduced viability (Migdałek et al. 2014) and the rate of vegetative spreading is very low due to a lack of long rhizomes. On the other hand, the presence of asexual ramets may also increase the chance of a hybrid persistence in the wild, since asexual ramets, like sexual ramets, are involved in the production of descendant ramets by clonal growth (Pliszko and Kostrakiewicz-Gierałt 2019).

The effect of habitat conditions on hybrid ramet clusters

In many species of *Solidago*, the development of synflorescences depends on the length of the shoots (Hartnett 1990; Schmid et al. 1995; Rosef et al. 2020). Therefore, it can be assumed that factors affecting shoot growth have a direct impact on the appearance of sexual and asexual ramets in *S.* ×*niederederi*. Our results suggest that the structure of ramet clusters in populations of *S.* ×*niederederi* is affected by elevation, soil pH and share of sand in the soil. According to Pliszko and Kostrakiewicz-Gierałt (2019), the number of descendant ramets in *S.* ×*niederederi* is positively correlated with the number of maternal ramets and the type of clonal cluster affects the number of descendant ramets. Nevertheless, it is important to test how the composition and number of ramets in individual clones change from one season to another in terms of changing environmental conditions to better understand the population dynamics and age structure of *S.* ×*niederederi*.

Effects of habitat conditions and type of ramet clusters on the length and biomass of shoots and synflorescences in hybrid populations

By achieving a sufficient height, biomass or ramet density, *Solidago* species can enter the generative phase or effectively compete for environmental resources or defend themselves against herbivores and pathogens (Cain et al. 1991; Schmid 1994; Schmid et al. 1995; Szymura and Szymura 2016). High elevation negatively affects the size of flowering shoots or synflorescences in the *Solidago* species (Szymura and Szymura 2013; Moran et al. 2017). Surprisingly, we found that sexual ramets of the hybrid were longer and heavier at higher elevation (S sites), while the length and biomass of synflorescences were similar in both groups of sites. Moreover, there was a positive correlation between the biomass of synflorescences in mixed clusters and elevation in NE sites. Nevertheless, considering that the elevation in study sites was low and narrowly ranged (160–540 m), it is important to test the effect of elevation in the future concerning populations located in mountainous regions. On the other hand, sometimes even a small-elevation gradient may negatively affect biomass allocation to sexual reproduction in clonal plants (Chen et al. 2015).

Apparently, the proportion of sand in the soil positively affects the length of asexual ramets in mixed clusters, whereas the soil pH can negatively affect the biomass of sexual and asexual ramets in mixed clusters, as well as the length and the biomass of synflorescences in mixed clusters. Moreover, the content of P_2O_5 positively affects the biomass of asexual ramets in asexual clusters of the hybrid populations. Interestingly, Karpavičienė and Radušienė (2016) found no effect of soil pH and content of organic C and P_2O_5 in the soil on maximal shoot height in *S.* ×*niederederi*, suggesting that a lack of correlation between the soil chemical composition and height of ramets can be explained by the variation of other environmental factors, such as water availability and competition.

Sexual ramets of *S.* ×*niederederi* were longer in sexual than in mixed clusters, confirming the results obtained in the previous study (Pliszko and Kostrakiewicz-Gierałt

2019). Moreover, the length of asexual ramets was negatively affected by the total number of ramets in mixed clusters in NE sites, the length of sexual ramets was negatively affected by the number of sexual ramets in mixed clusters in S sites and the biomass of sexual ramets was negatively affected by the total number of ramets in mixed clusters in S sites. As a comparison, in a 4-year pot experiment, Szymura and Szymura (2015) noticed that new ramets of *S. canadensis* and *S. virgaurea* located in the periphery of the clone were usually lower in height than old ramets placed in the centre of the clone, leading to a decrease of the average height of plants noted during the fourth year. Moreover, Cheng et al. (2021) found that the height and abundance of *S. canadensis* had no significant effect on its reproductive allocation, but individuals with higher total biomass can allocate more resources to sexual reproduction. Nevertheless, we did not find any significant correlation between the size of synflorescences and the number of sexual ramets in sexual and mixed clusters, in NE and S sites in Poland.

The response of the hybrid and its parental species to site conditions in the size of sexual ramets and synflorescences

Solidago ×*niederederi* and its parental species significantly differed from each other in the length of sexual ramets. Moreover, *S. canadensis* had longer sexual ramets in S than in NE sites. Surprisingly, the length of synflorescence was similar in the hybrid and its parental species with no effect of site. In contrast, Karpavičienė and Radušienė (2016) reported that the hybrid was different from *S. canadensis* and *S. virgaurea* in the length of synflorescence, but both parental species had similar length of synflorescence. On the other hand, Szymura and Szymura (2013, 2015) found differences in shoot height and synflorescence length between *S. canadensis* and *S. virgaurea*. In Europe, populations of *S. canadensis* are morphologically variable depending on habitat conditions, latitude and age of the clones (Weber 1997). Similarly, Kiełtyk and Mirek (2014) found a great morphological variation in shoot height and synflorescence length in *S. virgaurea* along an elevation gradient in Poland. Interestingly, we evidenced that the biomass of sexual ramets and synflorescences significantly differed between the *S.* ×*niederederi* and its parental species and the hybrid achieved higher biomass of synflorescences in S sites than in NE sites. Nevertheless, it should be pointed out that significant differences in biomass of synflorescences between the NE and S sites were not confirmed for a large number of sexual ramets, determined for all sexual and mixed clusters in the studied hybrid populations (shown in the above subsection). Therefore, the sample size most likely affected the results, making it difficult to draw firm conclusions.

Generally, invasive *Solidago* species (including *S. canadensis*) produce higher biomass than native *S. virgaurea* (Szymura and Szymura 2015; Szymura et al. 2019). Furthermore, *S. canadensis* invests more biomass in stems and leaves than in rhizomes, whereas the biomass of *S. virgaurea* is remarkably contributed to by synflorescences (Szymura and Szymura 2015). Interestingly, Szymura and Szymura (2016) demonstrated that *S. canadensis* is more competitive than *S. virgaurea*, because it achieved a higher percentage of flowering ramets when grown with *S. virgaurea* than when grown

in monoculture. Additionally, *S. virgaurea* showed a decrease in the percentage of flowering ramets when it was grown in combination with other species (Szymura and Szymura 2016). However, the above-mentioned authors suggested that the dominance of *S. canadensis* over native plant species may be less pronounced in a low-resource environment or disturbed places and the disturbance may also enhance the ability of *S. virgaurea* to persist in plant communities, despite its lower competitiveness. Considering the biomass allocation to flowering shoots and synflorescences, it can be assumed that the hybrid has more or less similar competitive abilities to its parental species, depending on the habitat conditions. Nevertheless, further study is needed to resolve the competitive abilities of the hybrid concerning the physiological and reproductive aspects of its performance in various habitats.

Conclusions

The structure of clones in hybrid populations most likely reflects differences in their age and habitat conditions. Sexual clusters dominate in hybrid populations, while the highest number of ramets is found in mixed clusters. In NE sites, the number of sexual ramets in mixed clusters is positively influenced by the share of sand, while in S sites, the number of asexual ramets in mixed clusters and the number of asexual ramets in asexual clusters are positively influenced by soil pH. Moreover, the length and biomass of ramets and synflorescences do not increase with the number of ramets in the individual clusters. *Solidago ×niederederi* seems to be a strong competitor for its parental species by achieving similar biomass of sexual ramets and synflorescences. However, other factors related to competition (e.g. photosynthesis capacity, growth rate, biomass allocation to underground parts, defence) under different environmental conditions should be investigated to better understand the naturalisation and invasive potential of the hybrid.

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References

Ayres DR, Zaremba K, Strong DR (2004) Extinction of a common native species by hybridization with an invasive congener. Weed Technology 18(sp1): 1288–1291. https://doi.org/10.1614/0890-037X(2004)018[1288:EOACNS]2.0.CO;2

Baranová B, Troščáková-Kerpčárová E, Gruľová D (2022) Survey of the *Solidago canadensis* L. morphological traits and essential oil production: aboveground biomass growth and abun-

dance of the invasive goldenrod appears to be reciprocally enhanced within the invaded stands. Plants 11: e535. [18 pp.] https://doi.org/10.3390/plants11040535

Cain ML, Carson WP, Root RB (1991) Long-term suppression of insect herbivores increases the production and growth of *Solidago altissima* rhizomes. Oecologia 88(2): 251–257. https://doi.org/10.1007/BF00320819

Calvo-Baltanás V, Wang J, Chae E (2021) Hybrid incompatibility of the plant immune system: an opposite force to heterosis equilibrating hybrid performances. Frontiers in Plant Science 11: e576796. [26 pp.] https://doi.org/10.3389/fpls.2020.576796

Chatzistathis T, Therios I (2013) How soil nutrient availability influences plant biomass and how biomass stimulation alleviates heavy metal toxicity in soils: the cases of nutrient use efficient genotypes and phytoremediators, respectively. In: Matovic MD (Ed.) Biomass Now – Cultivation and Utilization. IntechOpen (London): 427–448. https://doi.org/10.5772/53594

Chen C, Chen H, Shan J-X, Zhu M-Z, Shi M, Gao J-P, Lin H-X (2013) Genetic and physiological analysis of a novel type of interspecific hybrid weakness in rice. Molecular Plant 6(3): 716–728. https://doi.org/10.1093/mp/sss146

Chen X-S, Li Y-F, Xie Y-H, Deng Z-M, Li X, Li F, Hou Z-Y (2015) Trade-off between allocation to reproductive ramets and rhizome buds in *Carex brevicuspis* populations along a small-scale elevational gradient. Scientific Reports 5: e12688. [9 pp.] https://doi.org/10.1038/srep12688.

Cheng H, Wang S, Wei M, Wu B, Du D, Wang C (2021) Reproductive allocation of *Solidago canadensis* L. plays a key role in its invasiveness across a gradient of invasion degrees. Population Ecology 63(4): 290–301. https://doi.org/10.1002/1438-390X.12091

Daehler CC, Carino DA (2001) Hybridization between native and alien plants and its consequences. In: Lockwood JL, McKinney ML (Eds) Biotic Homogenization. Springer, Boston, 81–102. https://doi.org/10.1007/978-1-4615-1261-5_5

Daehler CC, Strong DR (1997) Hybridization between introduced smooth cordgrass (*Spartina alterniflora*; Poaceae) and native california cordgrass (*S. foliosa*) in San Francisco Bay, California, USA. American Journal of Botany 84(5): 607–611. https://doi.org/10.2307/2445896

Gudžinskas Z, Žalneravičius E (2016) *Solidago* ×*snarskisii* nothosp. nov. (Asteraceae) from Lithuania and its position in the infrageneric classification of the genus. Phytotaxa 253(2): 147–155. https://doi.org/10.11646/phytotaxa.253.2.4

Hartnett DC (1990) Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. Oecologia 84(2): 254–259. https://doi.org/10.1007/BF00318281

Jaźwa M, Jędrzejczak E, Klichowska E, Pliszko A (2018) Predicting the potential distribution area of *Solidago* × *niederederi* (Asteraceae). Turkish Journal of Botany 42: 51–56. https://doi.org/10.3906/bot-1703-17

Karpavičienė B, Radušienė J (2016) Morphological and anatomical characterization of *Solidago* ×*niederederi* and other sympatric *Solidago* species. Weed Science 64(1): 61–70. https://doi.org/10.1614/WS-D-15-00066.1

Kiełtyk P, Mirek Z (2014) Taxonomy of the *Solidago virgaurea* group (Asteraceae) in Poland, with special reference to variability along an altitudinal gradient. Folia Geobotanica 49(2): 259–282. https://doi.org/10.1007/s12224-013-9180-2

Li T, Huang L-X, Yi L, Hong L, Shen H, Ye W-H, Wang Z-M (2016) Comparative analysis of growth and physiological traits between the natural hybrid *Sphagneticola trilobata* × *calendulacea* and its parental species. Nordic Journal of Botany 34(2): 219–227. https://doi.org/10.1111/njb.00910

Migdałek G, Kolczyk J, Pliszko A, Kościńska-Pająk M, Słomka A (2014) Reduced pollen viability and achene development in *Solidago* × *niederederi* Khek from Poland. Acta Societatis Botanicorum Poloniae 83(3): 251–255. https://doi.org/10.5586/asbp.2014.025

Moran EV, Reid A, Levine JM (2017) Population genetics and adaptation to climate along elevation gradients in invasive *Solidago canadensis*. PLoS ONE 12(9): e0185539. https://doi.org/10.1371/journal.pone.0185539

Nilsson A (1976) Spontana gullrishybrider (*Solidago canadensis* × *virgaurea*) i Sverige och Danmark. Svensk Botanisk Tidskrift 70: 7–16.

Ostrowska A, Gawliński S, Szczubiałka Z (1991) Methods for analysis and evaluation of soil and plant properties. Catalogue. Institute of Environmental Protection, Warsaw, 334 pp.

Perera PCD, Szymura TH, Zając A, Chmolowska D, Szymura M (2021) Drivers of *Solidago* species invasion in Central Europe – Case study in the landscape of the Carpathian Mountains and their foreground. Ecology and Evolution 11(18): 12429–12444. https://doi.org/10.1002/ece3.7989

Pliszko A, Kostrakiewicz-Gierałt K (2017) Resolving the naturalization strategy of *Solidago* ×*niederederi* (Asteraceae) by the production of sexual ramets and seedlings. Plant Ecology 218(11–12): 1243–1253. https://doi.org/10.1007/s11258-017-0762-6

Pliszko A, Kostrakiewicz-Gierałt K (2018a) Flower-visiting insects on *Solidago* ×*niederederi* (Asteraceae): An observation from a domestic garden. Botanica Lithuanica 24(2): 162–171. https://doi.org/10.2478/botlit-2018-0016

Pliszko A, Kostrakiewicz-Gierałt K (2018b) The morphological intermediacy of *Erigeron* × *huelsenii* (Asteraceae), a hybrid between *E. acris* and *E. canadensis*. Turkish Journal of Botany 42(4): 543–550. https://doi.org/10.3906/bot-1711-27

Pliszko A, Kostrakiewicz-Gierałt K (2019) The importance of sexual, asexual and mixed ramet clusters in production of descendant ramets in populations of *Solidago* ×*niederederi* (Asteraceae). Biologia 74(8): 953–960. https://doi.org/10.2478/s11756-019-00233-y

Pliszko A, Zalewska-Gałosz J (2016) Molecular evidence for hybridization between invasive *Solidago canadensis* and native *S. virgaurea*. Biological Invasions 18(11): 3103–3108. https://doi.org/10.1007/s10530-016-1213-3

Polish Standard (1998) Soil and Mineral Soil Materials – Sampling and Determination of Particle Size Distribution. PN-R-04032. Polish Committee for Standardization, Warsaw, 12 pp.

Preacher KJ (2001, April) Calculation for the chi-square test: An interactive calculation tool for chi-square tests of goodness of fit and independence [Computer software]. http://quantpsy.org

Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. Taxon 53(1): 131–143. https://doi.org/10.2307/4135498

Rosef L, Ingerbrigtsen HH, Heegaard E (2020) Vegetative propagation of *Solidago canadensis* – do fragment size and burial depth matter? Weed Research 60(2): 132–141. https://doi.org/10.1111/wre.12395

Schmid B (1994) Effects of genetic diversity in experimental stands of *Solidago altissima* – evidence for the potential role of pathogens as selective agents in plant populations. Journal of Ecology 82(1): 165–175. https://doi.org/10.2307/2261395

Schmid B, Bazzaz FA, Weiner J (1995) Size dependency of sexual reproduction and of clonal growth in two perennial plants. Canadian Journal of Botany 73(11): 1831–1837. https://doi.org/10.1139/b95-194

Skokanová K, Šingliarová B, Španiel S, Hodálová I, Mereďa Jr P (2020) Tracking the expanding distribution of *Solidago* × *niederederi* (Asteraceae) in Europe and first records from three countries within the Carpathian region. BioInvasions Records 9(4): 670–684. https://doi.org/10.3391/bir.2020.9.4.02

Skokanová K, Šingliarová B, Španiel S, Mereďa Jr P, Mártonfiová L, Zozomová-Lihová J (2022) Relative DNA content differences reliably identify *Solidago* ×*niederederi*, a hybrid between native and invasive alien species. Preslia 94(1): 183–213. https://doi.org/10.23855/preslia.2022.183

Szymura M, Szymura TH (2013) Soil preferences and morphological diversity of goldenrods (*Solidago* L.) from south-western Poland. Acta Societatis Botanicorum Poloniae 82(2): 107–115. https://doi.org/10.5586/asbp.2013.005

Szymura M, Szymura TH (2015) Growth, phenology, and biomass allocation of alien *Solidago* species in central Europe. Plant Species Biology 30(4): 245–256. https://doi.org/10.1111/1442-1984.12059

Szymura M, Szymura TH (2016) Interactions between alien goldenrods (*Solidago* and *Euthamia* species) and comparison with native species in Central Europe. Flora 218: 51–61. https://doi.org/10.1016/j.flora.2015.11.009

Szymura M, Szymura TH, Rajsz A, Świerszcz S (2019) Is phenotypic plasticity an explanation for the invasiveness of goldenrods (*Solidago* and *Euthamia*) in Europe? Plant Species Biology 34(3): 73–84. https://doi.org/10.1111/1442-1984.12236

Upadhyay H, Juneja A, Turabieh H, Malik S, Gupta A, Bitsue ZK, Upadhyay C (2022) Exploration of crucial factors involved in plants development using the Fuzzy AHP Method. Mathematical Problems in Engineering 4279694: 1–9. https://doi.org/10.1155/2022/4279694

Vallejo-Marín M, Hiscock SJ (2016) Hybridization and hybrid speciation under global change. The New Phytologist 211(4): 1170–1187. https://doi.org/10.1111/nph.14004

Vilà M, Weber E, D' Antonio CM (2000) Conservation implications of invasion by plant hybridization. Biological Invasions 2(3): 207–217. https://doi.org/10.1023/A:1010003603310

Volery L, Blackburn TM, Bertolino S, Evans T, Genovesi P, Kumschick S, Roy HE, Smith KG, Bacher S (2020) Improving the Environmental Impact Classification for Alien Taxa (EICAT): a summary of revisions to the framework and guidelines. In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM (Eds) Frameworks used in Invasion Science. NeoBiota 62: 547–567. https://doi.org/10.3897/neobiota.62.52723

Weber E (1997) Morphological variation of the introduced perennial *Solidago canadensis* L. *sensu lato* (Asteraceae) in Europe. Botanical Journal of the Linnean Society 123(3): 197–210. https://doi.org/10.1111/j.1095-8339.1997.tb01413.x

Werner PA, Bradbury IK, Gross RS (1980) The biology of Canadian weeds. 45. *Solidago canadensis* L. Canadian Journal of Plant Science 60(4): 1393–1409. https://doi.org/10.4141/cjps80-194

Wu X, Liu Y, Zhang Y and Gu R (2021) Advances in research on the mechanism of heterosis in plants. Frontiers in Plant Science 12: e745726. [14 pp.] https://doi.org/10.3389/fpls.2021.745726

Zarzycki K, Trzcińska-Tacik H, Różański W, Szeląg Z, Wołek J, Korzeniak U (2002) Ecological Indicator Values of Vascular Plants of Poland. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 183 pp.

Supplementary material I

Supplementary details on study sites

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Data type: tables (word document)

Explanation note: table S1: Characteristics of study sites; table S2: The mean (± SD) values of soil parameters of the study sites.

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